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THE
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A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.L.S.,

ASSISTANT PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON.

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AND

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THE
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ON STIMULUS AND MECHANISM AS FACTORS
IN ORGANISATION.¹

BY J. BRETLAND FARMER, F.R.S.

I SUPPOSE it may be taken for granted that in the study of plants, as in other sciences, the ultimate aim of all enquiry is to establish a clear connection between cause and effect. The earlier stages in the enquiry consist in describing and classifying the effects or phenomena themselves, but there are probably few investigators who remain content with these efforts alone. In order to gain a wide comprehension of the phenomena it is essential that the factors that underly them shall be convertible into chemical and physical expressions, since in this way only is there any apparent chance of penetrating the temple in which the secrets of life are so securely guarded,

It must be confessed that most of the attempts in this direction have met with but scant measure of success. The hypotheses have often turned out to be erroneous and the theories destitute of any solid basis. But this circumstance does not affect the essence of the enquiry, nor indeed even its method. It is—or ought to be—a truism that the value of any hypothesis stands not in a necessarily direct relation to its final correctness, but rather depends upon the extent to which it welds together, even temporarily, cognate facts so as to suggest new lines of enquiry. No one doubts the value of the atomic theory, though of late there have not been wanting numerous assailants of this fundamental doctrine; and although perhaps few naturalists would be prepared to assert to-day with the same confidence that would have shown twenty years ago, that we have got to the bottom of the question as to the origin of species, nevertheless, history will assuredly preserve the great Darwinian Theory as one of the most precious landmarks in the advance of science and philosophy, whether it should ultimately turn out that

¹ A lecture delivered before Section K of the British Association, Southport, 1903.

comes to occupy a central position in the cell-cavity. At maturity of the cell this *primary nucleus* divides into two daughter-nuclei, each of which travels to one end of the sac. Then each divides by two successive divisions until four nuclei are formed at each end of the sac. One of these four from each end then travels to the centre of the sac, and, sometimes before, sometimes after, fertilisation takes place, these two *polar nuclei* fuse together to form the *definitive* or *secondary nucleus* of the embryo-sac. Meanwhile, each of the three nuclei at the micropylar end of the sac becomes invested with protoplasm enclosed by a delicate membrane; a pair of these cells, usually somewhat elongated, at the extreme end of the sac become the *synergidae*, while the third and larger cell becomes the *oosphere* or egg-cell. At the chalazal end of the sac three antipodal cells are formed, and these are often much more conspicuous than the cells at the micropylar end.

Hofmeister¹ considered that all the nuclei of the sac possessed primitively the same value and any one of them could develop into an embryo. The sole function of the antipodals was that of elaborating substances for the embryo.

Vesque² and Warming³ both regarded the embryo-sac as the product of fusion of two cells, and the four nuclei finally formed at each end of the sac were the representatives of the spores resulting from the divisions of these two spore-mother-cells.

Guignard⁴ held that all the cells in the sac were endosperm-cells; that the oosphere was a reduced archegonium; that the synergidae were endosperm-cells which had become adapted to a new function; and that the antipodals are either an organic residuum of the sac or a reduced prothallus; but he eventually regarded the prothallus as consisting of the sexual apparatus, antipodals and the two polar-nuclei.

Hartog⁵ believed that, as a result of two successive divisions of

¹ "Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen"; (Abhandl. d. Königl. Gesellsch. d. Wiss.; Vol. v., p. 671).

² "Développement du sac embryonnaire des Phanérogames Angiospermes"; Ann. d. Sciences Nat. Bot., ser. 6, Vol. vi., 1878.

"Nouvelles recherches sur le développement du sac embryonnaire"; Ditté, ser. 6., Vol. viii., 1879.

³ "Bemerkungen über das Eichen"; Bot. Zeit. 1874.

De l' Ovule"; Ann. d. Sci. Nat. Bot. ser. 6, Vol. v., 1878.

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Ann. d. Sci. Nat. Bot. ser. 6, Vol. xiii., 1882.

⁵ "Some Problems of Reproduction: a Comparative Study of Gametogeny and Protoplasmic Senescence and Rejuvenescence." (Quart. Journal Microsc. Science, Vol. xi., 1891).

the primary nucleus of the sac: "four prothallial cells are formed; of these two in the mean position [the mother-cells of the oosphere and upper polar-nucleus and of the uppermost antipodal and lower polar-nucleus respectively] are gametogonia, which by a mitotic division form four gametes, three functional, one arrested. The apical cell [of the original four] forms an archegonium reduced to a two-cellular neck [synergidae]; the basal cell forms two cells constituting a barren archegonium or mere prothallial cells" [the two lower antipodals]. The definitive or endosperm-nucleus he regards as a zygote formed by fusion of two gametes: the two polar nuclei.

Nawaschin in 1898 published the following epoch-making observations: that whenever a pollen-tube was seen in contact with the embryo-sac *both* male nuclei were observed in the latter, were seen to have an almost cylindric long-club-shaped appearance, and to exhibit a worm-like contortion; they lay free in the sac and so close together as to appear like a single body. One of these two nuclei travelled to the ovum, the other to the upper polar-nucleus, to which latter it became applied; both nuclei retained their worm-like character. During the time that the one male nucleus was becoming more and more closely applied to the ovum, the polar-nucleus, along with the second male nucleus with which it was in contact, travelled to the other polar-nucleus and became attached to the latter in the middle of the sac. All the nuclei remained separate and distinct until the prophases of their division. The second male nucleus, which by this time had lost its worm-like shape, was smaller, richer in chromatin, and possessed a coarser chromatin net-work than the polar nuclei, the lower of which latter is considerably larger than the upper. The character of the separate nuclei and composition of the nuclear groups were observed in a great number of fertilised ovules, so that there can be no doubt of the phenomenon being a constant one. Fusion of the three nuclei took place only after the prophases of division were completed; the same being true with regard to the fusion of the other male nucleus with that of the ovum. The formation both of the embryo and the endosperm was normal; in *Fritillaria tenella* the embryo, after reaching one-third of its size, died away, and the endosperm became absorbed. The ripe seed of *Lilium Martagon* contained a normal embryo. Nawaschin believed that, from the peculiar shape of the two male nuclei in these plants, they possess an independent movement like that of worms.

His theoretical conclusion with regard to these phenomena is that we have before us in these plants a species of *polyembryony*, in the form of a pair of twin-embryos exhibiting a very dissimilar and unequal development, the one remaining thallus-like, in the form of the endosperm, and becoming eventually absorbed by the other. His view is based on the fact that the normal endosperm arises as the result of the fusion of one of the male nuclei with the *sister-cell of the ovum*, i.e., with one of the female nuclei; and that therefore we have as much right to speak of this fusion as a *sexual act* as in the case of the actual process of fertilisation itself. At a somewhat later date Nawaschin¹ observed "double fertilisation" in certain Dicotyledons. In the case of *Helianthus* the male nuclei were seen greatly to resemble spermatozooids, the polar nuclei were observed to fuse *before* fertilisation of the ovum, and the product of this fusion—the embryo-sac-nucleus—after copulation with the second spermatozoid was seen to divide rather earlier than was the case with the fertilised oosphere. In *Rudbeckia* similar phenomena occurred. Fusion of the polar-nuclei before fertilisation of the ovum was also observed in *Delphinium elatum*. It is an interesting fact that Merrel found elongated, spirally-twisted bodies (=spermatozooids) in the pollen grain of the Composite, *Silphium*.

Guignard essentially confirms Nawaschin's observations. He states as a result of his own labours on *Lilium Martagon* that union of both polar nuclei may precede their fusion with the vermiform sperm-nucleus and that the latter may subsequently become applied to *both* polar nuclei, but in some cases the sperm-nucleus was observed to fuse primarily with the antipodal polar-nucleus; more frequently however, copulation with the egg-polar-nucleus is the first process, because the latter is the first of the two met with by the sperm-nucleus as it passes down the sac. Guignard regards, in contradistinction to Nawaschin's view, the union or fusion of the sperm-nucleus with the polar nuclei as a case of *pseudo-fertilisation*, on the following grounds. In *true* fertilisation both sexual nuclei have the same reduced number of chromosomes, whilst the lower polar nucleus, as at any rate is known to be the case in *Lilium*, contributes a larger number of chromosomes to the fusion, with the result that the product of copulation of sperm and polar-nuclei possesses a greater number of chromosomes than does the fertilised ovum.

¹ "Ueber die Befruchtungsvorgänge bei einigen Dicotyledoneen" (Berichte der deutsch. Bot. Gesellschaft, vol. 18, 1900).

Some further observations by Guignard¹ on *Tulipa Celsiana* and *T. sylvestris* revealed the fact that the various nuclei of the embryo-sac in these two plants were very irregularly arranged and more or less similar in appearance. The lower polar nucleus, which is morphologically different from the upper one, being often larger and with denser granulations, is situated at the base of the sac, below the antipodal nuclei. The antherozoids are elongated, but not spirally twisted, and are both equivalent. The oosphere is first fertilised. The second sperm-nucleus was seen fusing with the upper of the two polar-nuclei, hence union between these latter is a late occurrence in these plants. The second sperm-nucleus and the two polar nuclei fuse together as three distinct individualities, which gradually become less and less marked and finally vanish. He observed that at the moment of division of the fertilised ovum the sac contained four endosperm-nuclei. The phenomena above described hold good for the two species mentioned; but the different races of cultivated Tulips, on the contrary, agree in this respect with the Lily and *Fritillaria*.

This author further observed² "double fertilisation" in several other orders of plants, such as Compositae, of which five or six genera were investigated, with the result that his observations largely coincided with those of Nawaschin on *Rudbeckia*. In Ranunculaceae³ the genera *Caltha*, *Ranunculus*, *Helleborus*, *Anemone*, *Clematis* and *Nigella* were examined. The two male-nuclei in these plants are spindle-shaped while within the pollen-tube, becoming elongated as they pass into the sac; they rapidly fuse with the two nuclei of the sac. In *Nigella damascena* the larger size of the male nucleus which fuses with secondary nucleus of the sac is correlated with the fact that the latter divides *before* the fertilised ovum. At the time of endosperm-formation the fusion of the male and female nuclei in the oosphere is not completed, and even after fifty endosperm-nuclei are formed in the sac the ovum remains still undivided. The same phenomenon was observed in *Anemone nemorosa*. Quite recently⁴ the order Cruciferae revealed the same

¹ "L'appareil sexual and la double fécondation dans les tulipes" (Annales des sciences naturelles, ser. 8, vol. xi., 1900).

² "Nouvelles recherches sur la double fécondation chez les végétaux angiospermes" (Comptes Rendus de l'Acad. des Sciences, vol. 131, 1900).

³ "La double fécondation chez les Renonculacées" (Journal de Botanique, Dec. 1901).

⁴ "La double fécondation chez les Crucifères" (Journal de Botanique, Nov. 1902).

phenomenon of "double fertilisation" which is probably of universal occurrence in Angiosperms. In *Capsella* fusion of the polar-nuclei was observed to take place at a very late period, yet division of the fertilised secondary nucleus was sometimes seen to be well-nigh complete while the other antherozoid is still in contact with the nucleus of the oosphere. Division of the ovum occurs after formation of the first four endosperm-nuclei. In *Lepidium* there is a slightly earlier fusion of the polar-nuclei.

But Miss Ethel N. Thomas¹ distinguished herself through being the first to publish an account of the process of "double fertilisation" in Dicotyledons, an undertaking to which she was prompted by Miss Ethel Sargent, who had, by her own original observations, confirmed the work of Nawaschin and Guignard on the Liliaceae. Miss Thomas found that in *Caltha palustris* the two polar-nuclei were usually completely fused before the entrance of the pollen-tube. The generative nuclei when emitted are very minute and are either oblong, or lens-, dumb-bell-, or straight S-shaped. She received the impression that the first generative nucleus emitted was the one which fertilised the polar-nuclei, for the latter process always appeared to be much more advanced than that of the fertilisation of the oosphere, and she suggests that this may partly account for the fact of the phenomenon being overlooked for so long. The vermiform nucleus which fertilises the polar nuclei, increases greatly in size, while this is not the case with the other sperm-nucleus.

The epoch-making experiments on the *hybrid fertilisation of endosperm* conducted by De Vries² in 1898 afford a most striking illustration of the reality, and, in certain cases, the far-reaching consequences of the phenomenon of "double fertilisation," this latter, indeed, alone affording an explanation of the facts involved in those experiments. De Vries in 1898 possessed forty specimens of the variety of the Maize-plant whose grains contain a *sugary* endosperm; in the following year he obtained from these grains a second generation of sixty plants producing sixty-seven spikes full of grains all containing sugar only. It is therefore clear that the plants destined for his experiments, being the offspring of the same original lot, would, if fertilised with their own pollen, have yielded pure spikes of sugared grains. The hybrid fertilisation took place in August, 1898. At the beginning of the month, before flowering

¹ "On the Presence of Vermiform Nuclei in a Dicotyledon." —
"Double Fertilisation in a Dicotyledon—*Caltha palustris*"
(Annals of Botany, Sept. 1902).

² "Sur la fécondation hybride de l'endosperme chez le Maïs"
Revue générale de Bot., vol. xii, 1900).

took place, he cut off the greater part of each male inflorescence. On emergence of the stigmas from their bracts he powdered them at intervals with pollen of a variety of Maize possessing grains with *starchy* endosperm, yet without entirely preventing fertilisation by the pollen emanating from the lower branches of their own male inflorescences. The result was ten large spikes full of grains. Each spike bore two kinds of grains, the greater number being *starchy* like the father, the remainder *sugary* like the mother. These last were largely due to auto-fertilisation, which was proved by sowing a portion of them in 1899, when they reproduced the *sugary* variety of the mother. The *starchy* grains were *hybrids*, as well in their endosperms as in their embryos. The endosperm exhibited entirely the character of the father, being well filled with starch and containing no visible trace of sugar, being a chalky-white within, and having a smooth external surface, without the wrinkles so characteristic of the grains of the *sugary* variety. It was clear that these paternal characters had been communicated by the second spermatozoid of the pollen-tube. In order to prove the hybrid nature of the *embryos* of these grains he sowed a portion of them in 1899 and allowed the plants to be fertilised by their own pollen. He obtained a crop of thirty-two plants yielding thirty-five spikes, rich in grains. All these spikes were of mixed nature, about a quarter of the grains were *sugary*, the three remaining quarters being *starchy*; the former had reverted to the character of the grandmother, the latter exhibited that of the father and grandfather. The *starchy* grains of his crossed spikes of 1898 were therefore *hybrids*, capable of reproducing the types of their two parents. In all these spikes there occurred no grains of intermediate character, half *sugary*, and half *starchy*.

W. O. Focke, in his great work "Die Pflanzenmischlinge," which contains a résumé of all the experiments conducted by Körnicke, F. Hildebrand and De Vries, proposed the term "*xenia*" for all cases in which an influence of the pollen on the hereditary characters of the fruit or grain *outside the embryo* has been either determined or presumed. About the same time as, or a little later than De Vries' work, some detailed investigations and experiments were carried out by Correns,¹ as a result of which he established several valuable and important corollaries for which we have no space here. He at first imagined that *xenia* was due to a fusion of half the generative nucleus (as a result of division of the latter) with

¹ "Untersuchungen über die Xenien bei *Zea Mais*" (Berichte der deutsch. bot. Gesellschaft, 1899), etc.

the secondary nucleus of the sac. The process he regards as a case of of true fertilisation inasmuch as the Maize-grain, produced as a result of pollination by another race, contains, besides the bastard-embryo, a bastard-endosperm. A second possible explanation offered by him is that the bastard-embryo exercises an *enzymatic* action on the endosperm, this being not so unlikely, seeing that it is merely a question of formation of colouring-matter or of closely-allied reserve-stuffs. It is to be noted that xenia-formation has been observed by Giltay in the Rye, where it corresponds to one of the special cases in the Maize. Correns points out that cases in which races or closely-allied species exhibit essential differences in the character of the endosperm, are, unfortunately, of rare occurrence.

The publication of Nawaschin and Guignard's observations solved the whole problem of xenia or hybrid endosperm-formation, for it is manifest that a fusion of the second male or sperm-nucleus emanating from the pollen of the foreign race with the definitive or secondary nucleus of the embryo-sac, the division of which latter, as we know, invariably gives rise to the endosperm, would supply all the necessary conditions under which a hybrid endosperm could be produced; for just as the fertilised ovum gives rise on division to an embryo combining in itself the characters of the two parents from which the first generative nucleus and that of the oosphere respectively proceeded, precisely the same will be true of the product of division of the definitive nucleus "fertilised" by the second generative nucleus of the pollen-tube.¹

We have reserved until last the observations or theoretical considerations of the two authors who appear, in our opinion, to shed the brightest light upon this most interesting problem of "double fertilisation." To our thinking Strasburger² in this matter maintains his great reputation as a leader in all that concerns investigation into the wonderful developmental history of the embryo-sac. He himself observed "double fertilisation" in several Orchids and in *Monotropa Hypopitys*. He regards the passage through the embryo-sac of the second sperm-nucleus (which, in the plants examined by him, did not always exhibit a worm-like shape) as probably of a *passive* nature. His explanation of the whole course of events in the embryo-sac is as follows:—The prothallus-formation in the embryo-sac of all Angiosperms is divided into two

¹ For an account of Correns' work and its relation to Mendel's laws of hybridism. see THE NEW PHYTOLOGIST, vol. I., 1902, p. 103.. *et seq.*

² "Einige Bemerkungen zur Frage nach der 'doppelten Befruchtung' bei den Angiospermen" (Botanische Zeitung, 1900).

distinct stages,¹ the first stage consists in the formation of the synergids and antipodal cells; after the third division, resulting in the production of the eight nuclei in the sac, these latter no longer possess the power of dividing further; hence an interruption in the process of prothallus-formation, during which interval fertilisation of the ovum takes place. But it can be readily seen that, should this latter function fail to be performed, the formation of endosperm (prothallus) would entail a great waste of energy, hence we find that in the vast majority of cases the latter is made *dependent on the former*. But, and here we reach the core of the whole problem, inauguration of the second stage of prothallus-formation must be effected by some *fresh stimulus*; and this is afforded by the second sperm-nucleus, which, through fusion with the definitive nucleus of the sac, increases the nuclear substance of the latter, inducing thereby the divisions which constitute the second stage of prothallus- or endosperm-formation to proceed rapidly. The interesting results obtained in Maize-cultures, which led Correns to entertain the mistaken idea that this "double fertilisation" constituted a process of true fertilization, could hardly have been different when fusion between the sperm and the definitive nucleus takes place.

The whole character of the endosperm is antagonistic to the idea of its being a second "nutritive embryo." Yet he suggests that the process which now consists merely in a stimulus may in the course of time have been degraded from a process of true fertilisation.

Strasburger cites cases where, *in the absence of fertilisation*, the formation of endosperm may take place, *e.g.*, in *Cœlebogyne* (where adventitious embryos occur), *Ranunculus multifidus*, *Antennaria alpina* (in which each polar-nucleus divides independently), and *Balanophora elongata* (in which the *upper polar-nucleus only* divides). He mentions that these cases may possibly represent reversions to the time when the sac became filled with a prothallus before fertilisation.

Celakovsky,² the great Bohemian morphologist, adheres to the view put forward by Strasburger³ that the production of endosperm is "*a continuation of the original process of endosperm-formation which had been interrupted by the early appearance of fertilisation, all the*

¹ This view had also been expressed by Guignard in his early work on the embryo-sac.

² "Ueber den phylogenetischen Entwicklungsgang der Blüthe, &c.," Part II., p. 207 (Sitzungsberichte der königl. böhm. Gesellschaft der Wissenschaften in Prag, 1900).

³ Die Angiospermen und die Gymnospermen, 1879.

original nuclei of the sac corresponding to the prothallus, along with archegonia, in the Gymnosperms. This idea of a retarded prothallus-formation is confirmed by Karsten's observations on species of *Gnetum* in which a similar phenomenon occurs; but in these cases many free nuclei of the endosperm arise before fertilisation, while in Angiosperms only two such free nuclei (the polar nuclei) are present. In *Gnetum Gnemon*, where an abundant endosperm is developed in the lower part of the embryo-sac before fertilisation, the *later-formed* rudimentary endosperm aborts, while in the Angiosperms, on the contrary, this is what happens to the reduced *primary* endosperm, while the later-formed endosperm persists. In view, therefore, of the fact that the secondary persistent endosperm of Angiosperms is the homologue of the secondary aborting endosperm of *Gnetum Gnemon*, and that there can be no possible question of the latter partaking of the nature of an embryo, it follows that the former also can never be identified with an embryo, and *cannot therefore correspond to the second zygote [the product of fertilisation] of Gnetum Gnemon.*¹

As regards the activities of the second sperm-nucleus, Celakovsky points out that if this latter fused *merely* with the sister-nucleus of the ovum, *viz.*, the upper polar-nucleus, the product of fusion could hardly be regarded in any other light than as a twin-product with the egg. But the idea of a true sexual act in connection with the process which actually does occur, *viz.*, fusion with the product of union of both polar-nuclei, is not to be entirely rejected. The first thing to discover is what this "double-nucleus" with which the sperm-nucleus has united really is, and especially to what *cell* it belongs. *The cell-nucleus of the megaspore* or embryo-sac, having been resolved into its posterity of eight nuclei, becomes, through fusion of the polar-nuclei, *regenerated*, and its original energy restored, this being necessary in order that there might be a rapid continuation of the cell-formation which, begun by the primary embryo-sac nucleus, had later been interrupted. This secondary nucleus also assumes once more the position in the centre of the sac which had previously been occupied by the primary nucleus. On this hypothesis the endosperm is *not a sister-product or twin with the embryo*, but the retarded portion of the mother-structure: the prothallus. Inasmuch as a sperm-nucleus fuses with the polar-nuclei it must be assumed that these latter have assumed an actual female character, for otherwise the attraction of the male nucleus

¹ See Lotsy's work on *Gnetum Gnemon*,

to the same would be, in the light of our present knowledge, incomprehensible. "The influence of the male nucleus on the fusing polar-nuclei is probably a necessary factor in the case, consisting in a stimulation of the female double-nucleus to further activity, by affording it a renewed supply of energy, while at the same time, as the experiments with the Maize appear to shew, characters from the male side are inevitably transferred to the regenerated megaspore-nucleus," Celaskovsky states finally that he cannot admit that the originally normal process of fertilisation, the product of which is an embryo, has become *degraded* to a process of mere pseudo-fertilisation and the embryo to an endosperm-thallus, but must regard *the new sexual act as phylogenetically an advanced process* ("Höherbildung"); for the original asexually-formed prothallus (in Pteridophytes, Gymnosperms, and possibly in many Angiosperms) becomes, in its second retarded stage (as in the case of certain, if not all, Angiosperms), sexually produced like the embryo.

To our own mind, and as far as we can judge, the view set forth by Celaskovsky affords a quite satisfactory solution of the whole problem; it is nevertheless desirable that further observations of fact should be forthcoming.

W. C. W.

ON ASEXUAL REPRODUCTION
AND REGENERATION IN HEPATICAE,

By F. CAVERS,

Yorkshire College, Leeds.

(WITH EIGHT FIGURES IN THE TEXT).

(Continued from page 133.)

Gemmae. In the Acrogynae the gemmae, which are usually unicellular or few-celled, are formed from the cells of the leaf and sometimes also from the superficial cells of the stem. Not only the ordinary lateral or foliage leaves, but the amphigastria, the male and female bracts ("perigonial" and "involucral" leaves), and even the perianth may bear gemmae. The process of gemma-formation may be confined to the margin of the leaf or to the tips of the lobes in a divided leaf, or it may encroach more and more upon the tissue of the leaf, until the latter is represented only by a cluster of loosely-connected gemmae. In a considerable number of forms (e.g., *Cephalozia bicuspidate*, *Kantia trichomanis*), the apex

of the main stem or of its branches often becomes entirely given over to the production of a rounded mass of gemmae; these gemmiferous shoots often grow erect and assume apparently radial symmetry, the amphigastria becoming here similar in form to the lateral leaves and like them producing strings or clusters of gemmae, whilst the shoot is terminated by a globular mass consisting of branched rows of gemmae (Fig. 6).

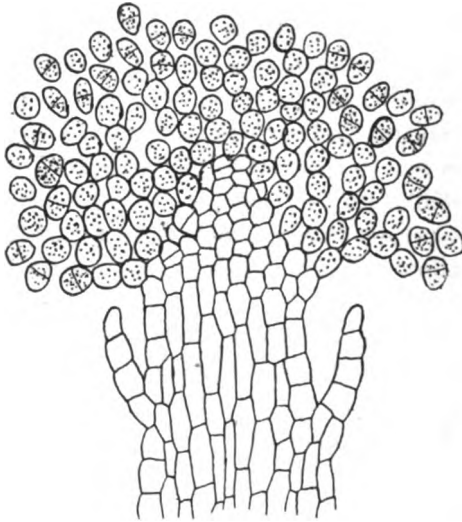


Fig. 6. *Cephaloxia bicuspidata*. Longitudinal section through the apex of an erect gemmiferous shoot, showing two of the reduced leaves and numerous gemmae, some arranged in branching chains. $\times 150$.

The gemmae may be either (1) uni- or bi-cellular bodies, formed singly or in chains and branched clusters on the margins of the leaves or the summit of the stem; or (2) discoid multicellular bodies arising on the margins or the surfaces of the leaves.

The uni- or bi-cellular gemmae are usually spherical or ovoid in form (Fig. 6), but sometimes they are tetrahedral (e.g., *Lophozia ventricosa*) or polygonal [e.g., *Diplophyllum albicans* (Fig. 7)]. In most cases they are green or yellowish in colour, but frequently they are red, brown, or purple (e.g., *Scapania nemorosa*).

Discoid gemmae occur in the families Stephaninoideae (*Radula*), Bellincinioideae (*Porella*), and Jubuloideae (*Frullania*, *Lejeunea*); whilst uni- or bi-cellular gemmae are found in all the remaining families, except the Pleurozioideae (*Pleurozia*). Gemmiferous species occur in the great majority of the Acrogynous genera, and it would appear that the production of gemmae plays

an important part in the propagation of these plants, especially in the case of species which are seldom found in fruit.

In the subjoined list, the principal characters of the gemmae are briefly noted. Except where otherwise stated, the species occur in the British Islands, the families being given in accordance with the system proposed by Spruce¹ and adopted by Schiffner.²

Fam. 1. *Epigoniantheae*. *Marsupella emarginata*. Gemmae ovoid, 1-2-celled, pale brown, on leaf-margins, especially those near top of stem.

Lophozia barbata, *L. intermedia*, *L. orcadensis*, *L. porphyroleuca*, *L. ventricosa*. G. triangular or polygonal, 2-3-celled, in brown masses on tips of uppermost leaves.

L. exsecta, *L. Helleriana*. G. ovoid, 1-3-celled in dark-red masses on uppermost leaves "In *L. exsectaeformis*, however, the gemmae are triangular and 1-celled."

L. heterocolpa. G. ovoid, 1-2-celled, in a large reddish mass at stem-apex, surrounded by uppermost leaves.

L. incisa. G. polygonal, 1-celled, in yellowish masses on the crowded terminal leaves.

L. minuta. G. ovoid, 1-celled, in small brown masses on the leaves of special slender shoots.

Lophocolea bidentata, *L. heterophylla*. G. occur either as isolated spherical or ovoid cells on leaf-margins, or as irregular masses on the upper leaves and the tops of erect shoots.

Mylia Taylora, *M. anomala*. G. ovoid or elongated, 1-2-celled, in dark-green masses on uppermost leaves, singly on the lower ones.

Fam. 2. *Trigonanthae*. *Cephaloxia bicuspidata*, *C. catenulata*, *C. dentata*, *C. divaricata*. G. spherical or ovoid, 1-2-celled, in light-green masses on the summit of erect shoots, and on margins of uppermost leaves (Fig. 6).

C. Francisci. G. triangular, 2-celled, in reddish masses on the tips of the uppermost leaves of slender shoots.

C. Starkii. G. ovoid, 1-2-celled, in brown masses on tips of upper leaves.

Nowellia curvifolia. G. spherical, 1-celled, scattered on margins of upper leaves.

Odontoschisma Sphagni, *O. denudatum*. G. spherical or ovoid, 1-2-celled, in masses at the ends of slender small-leaved branches.

¹ Spruce, R., *Hepaticae Amazonicae et Andinae*. Trans. Bot. Soc., Edinburgh, Vol. 15. 1885.

² Schiffner, V., *Hepaticae*. Engler u. Prantl, Nat. Pflanzenfamilien, Teil. I, Abt. 3, 1893.

Kantia trichomanis, *K. suecica*, *K. submersa*. G. spherical or ovoid, 2-celled, in a large globular green mass at the summit of an erect shoot, also scattered on the upper leaves and amphigastria.

Fam. 3. *Ptilidioideae*. *Ptilidium ciliare*. G. spherical or ovoid, 1-2-celled, scattered on the margins of the leaves, especially the uppermost ones.

Blepharostoma trichophyllum. G. spherical, 1-2-celled, formed in chains from the segments of the much-divided leaves, especially those near summit of shoot.

Trichocolea tomentella. G. as in *Blepharostoma*.

Fam. 4. *Scapanioideae*. *Scapania aequiloba*, *S. aspera*, *S. Bartlingii*. G. ovoid, 1-2-celled, in dark-green masses on margins of uppermost leaves.

S. compacta, *S. umbrosa*. G. elongated, 1-3-celled, in radiating chains forming a rounded yellowish mass at summit of stem, surrounded by the uppermost leaves.

S. crassiretis. G. ovoid, 1-celled, in brown masses on uppermost leaves.

S. irrigua, *S. undulata*. G. ovoid, 1-3-celled, in rounded light-green masses at the stem-apex, also scattered on uppermost leaves.

S. nemorosa. G. ovoid, 1-3-celled, in dark-brown masses on the tips of the upper leaves, sometimes also in a ball at the stem-apex.

S. resupinata. G. ovoid, 1-3-celled, in a reddish-brown ball at the stem-apex, also scattered on margins of uppermost leaves.

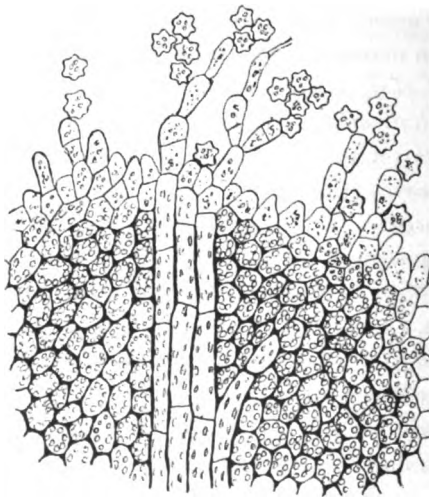


Fig. 7. *Diplophyllum albicans*. Upper portion of a leaf, showing formation of numerous small polygonal gemmae from the marginal cells. $\times 150$.

Diplophyllum albicans. G. polygonal, 1-celled, in yellowish clusters on the leaf-margin, towards the tips of the smaller upper and the larger lower lobes. Both the elongated cells of the "midrib" and the polygonal cells on each side of this take part in the production of the gemmae, the leaves often becoming eroded and truncated in consequence (Fig. 7).

Fam. 5. *Stephaninoideae*. In several species of *Radula*, the leaves frequently bear, either on the margin or the lower surface, scattered discoid gemmae, each consisting of a plate of cells, circular or oval in outline. The writer has followed the development of the gemmae in *R. complanata*. Each gemma arises from a single marginal cell, which grows in size and becomes further distinguished from the cells on either side by containing from one to four small brown oil-bodies, in addition to the large oil-body normally found in each of the leaf-cells in this species. These extra oil-bodies do not appear to arise by division or budding from the larger one, but are developed independently by segregation of the protoplasm to form a stroma, in which oil-drops soon appear. The cell then undergoes repeated divisions, the small oil-bodies passing into the newly-formed cells, so that ultimately each cell of the gemma contains one of these bodies, which becomes enlarged until it reaches about the same size as the oil body of the ordinary leaf-cell. The gemma is attached to the leaf-margin by a narrow base consisting of one or two cells, and shows on its distal margin a large apical cell, triangular in surface view, from which the young leafy shoot arises, when the gemma becomes detached and begins to germinate. Similar gemmae are found in *R. germana* and *R. Lindbergii*, which occur in Britain. In some tropical species of *Radula*, e.g., *R. tjiibodensis*, the gemmae are larger than in *R. complanata*, and some of the marginal cells are modified to form organs of attachment, regarded by Goebel¹ as rhizoids of arrested growth, by which the gemma fixes itself to the substratum (leaves and trunks of trees).

Fam. 6. *Pleurozioideae*. In this family, represented by the single genus *Pleurozia* (*Physotium*), gemmae do not appear to have been yet observed.

Fam. 7. *Bellincinioideae*. In *Porella rotundifolia*, from Brazil, Schiffner² figures discoid gemmae on the lower surface of the leaf, evidently resembling those of *Radula* and various *Lejeuneae*.

¹ Goebel, K., Epiphytische Farne und Muscineen. Ann. du jard. bot. de Buitenzorg, Vol. 7, 1887.

² Schiffner, V., Ueber exotische Hepaticae; Taf. 6, Fig. 2.

Fam. 8. *Jubuloideae*. In *Frullania dilatata*, gemmae are sometimes formed on the margins of the leaves, each consisting of four to six cells as a rule and being discoid or irregular in form. The outer surface of the perianth in this species bears numerous irregular outgrowths, each made up from two to five or six cells. These outgrowths may be regarded as gemmae, for the writer has found that when the whole or a portion of a perianth is isolated and kept under cultivation, some of them give rise to leafy shoots, either before or after becoming detached from the perianth. The caducous lobules of *F. fragilifolia* have already been described under the heading of adventive shoots, but these organs might reasonably be regarded as gemmae, since they become detached from the plant before giving rise to the new leafy shoot. In several of the Lejeuneae, there are produced discoid gemmae, similar to those of *Radula* in general form, but in some cases showing peculiar features. In *Thallosejeunea (Metzgeriopsis) pusilla*, a remarkable form discovered in Java by Goebel,¹ the vegetative portion of the plant consists of a repeatedly-branched thallus with toothed margins, whilst the sexual organs are borne on short leafy shoots each arising from the apex of a branch. The thallus bears on its upper surface and its margins numerous discoid gemmae, each consisting of an oval plate of cells, lying parallel with the surface of the thallus, to which it is attached by a short stalk-cell. The mature gemma consists of about twenty cells, arranged in a single layer, and shows two growing-points occupying opposite sides of the gemma and each showing a wedge-shaped apical cell. Similar gemmae are also found on the male and female bracts.

Discoid gemmae are formed on the leaves of *Cololejeunea calcarea* (Fig. 8), *C. minutissima*, *C. microscopca*, *Eulejeunea serpyllifolia*, and *Colurolejeunea calyptrifolia*, all of which occur in Britain. In some tropical forms described by Goebel, e.g., *Cololejeunea Goebelii*, *Odontolejeunea mirabilis*, the gemmae have two growing-points, as in *Metzgeriopsis*, and some of the marginal cells are modified to form organs of attachment. The writer has followed the development of the gemmae in *Cololejeunea calcarea* (Fig. 8), which are sometimes found in abundance on the lower surfaces of the leaves, each consisting when mature of a circular or oval disc, one cell in thickness, attached to the leaf by a single stalk-cell which is inserted at the centre of the lower surface of the gemma.

¹ Loc. cit., p. 54, Tab. 6--8; also Schiffner, V., *Morphologie und systematische Stellung von Metzgeriopsis pusilla*. Oesterr. botan. Zeitschrift, 1893, p. 4 of reprint.

The gemmae are formed on both the larger upper lobe and the smaller lower lobe of the leaf; the two lobes are sharply folded on each other, so as to form a kind of pocket, in which the writer frequently found a number of free gemmae. Probably the gemmae, on becoming loosened from their unicellular stalks, which usually

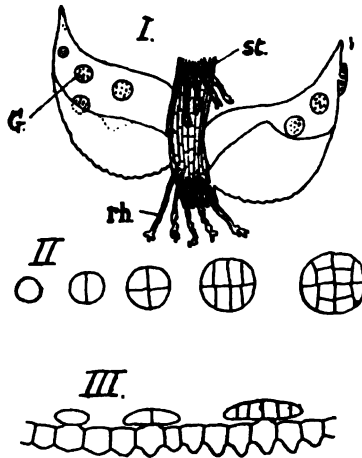


Fig. 8. *Cololejeunea calcarca*. I. Part of a plant, seen from ventral surface, showing two leaves with gemmae (G.); st., stem; rh., rhizoids. $\times 30$. II. Stages in development of gemma, as seen in surface view. $\times 100$. III. Part of leaf in vertical section, showing three developing gemmae. $\times 100$.

remain behind and mark the spots where gemmae have been formed, accumulate in the basal pocket of the leaf, from which they may ultimately be washed out by rain-drops. In a few cases, these free gemmae had already begun to germinate within the basal sac. The cell-divisions in the developing gemma show great regularity (Fig. 8, II., III.), the marginal cells being all of nearly the same size, so that here there does not appear to be any definite growing-point in the mature gemma, as in *C. Goebelii*, but the young shoot may arise from any one of the marginal cells.

III. *Anthocerotales*. In *Anthoceros laevis*, adventive branches are sometimes formed, each arising from a single superficial cell of the thallus. The occurrence of gemmae has been described in *A. glandulosus* and in some species of *Dendroceros* (*D. cichoraceus*, *D. javanicus*). In *Dendroceros*, the gemmae are small rounded or irregular bodies, each formed from a single cell of the thin wings or leaves. In *Anthoceros glandulosus*, Ruge¹ found that each gemma arose as a club-shaped outgrowth from a superficial cell, which

¹ Ruge, G., Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, Flora, 1893, Heft 4; p. 36 of reprint.

divided repeatedly by transverse walls, giving rise to a row of cells. The uppermost cell then became enlarged and divided by a longitudinal wall. Repeated transverse and longitudinal divisions then occurred in this swollen terminal portion, in the interior of which an intercellular space was formed by splitting of the primary longitudinal wall. This closed sac then became filled with mucilage, whilst two other mucilage-cavities were also formed immediately above the insertion of the stalk of the gemma, but each of these opened externally by a slit and resembled the ordinary *Nostoc*-cavities of the thallus. The tubers which have been described in various exotic species of *Anthoceros*, and more recently by Goebel¹ in *A. laevis* itself, may be regarded as organs of asexual propagation, especially when several tubers are borne on one plant. These tubers, as in the case of *Riccia*, *Fossombronia*, *Geothallus*, and *Petalophyllum*, arise as swellings on the lower surface of the thallus, near the margin; their cells contain reserve food-materials, and they are adapted for carrying the plant over unfavourable climatic periods and of germinating to form new plants.

REGENERATION OF THE GAMETOPHYTE.

Necker appears to have been the first to describe the process of gametophytic regeneration in Hepaticae. In his "Physiologia Muscorum," published in 1774, he states (p. 27) that he cut the thallus of *Marchantia polymorpha* and of *Fegatella conica* into numerous small pieces, which he cultivated on soil and watered daily. In about a month, he observed outgrowths arising from many of the fragments, each outgrowth at length giving rise to a new plant. He obtained similar results in his experiments with *Ricciella fluitans* and with a number of leafy Jungermanniales. These observations of Necker's appear to have been entirely overlooked by later writers on the subject.

In 1885 Vöchting² published an important paper in which he showed that the gametophyte of *Lunularia* and *Marchantia* possesses in an extraordinary degree the property of regeneration. On cutting out portions of the thallus or of the sexual receptacles and keeping them under cultivation, he obtained numerous adventive outgrowths, each arising from a single cell. Even when portions of the thallus were minced up into very small fragments, many of the latter were found to give rise to new shoots. Vöchting therefore concluded that in the gametophyte of these Liverworts, every cell

¹ Goebel, K., Organographie der Pflanzen, p. 294.

² Vöchting, H., Ueber die Regeneration der Marchantieen. Jahrb. für wiss. Botanik, Band 16, Heft 3, 1885.

is capable of regenerating the entire plant, provided that it retains its living protoplasmic contents and is exposed to favourable conditions. As already stated, naturally-occurring adventive outgrowths have been observed on the female receptacles of *Marchantia* and *Dumortiera*, but such instances of regeneration in the specialised sexual shoots of the Marchantioideae are extremely rare in nature, though the formation of adventive shoots is readily induced when the antheridiophores or archegoniophores, or portions of these, are severed from the rest of the plant and kept under cultivation. Schostakowitsch¹ has confirmed and extended the observations of Vöchting. He obtained adventive growths from cultures of excised portions of the thallus in *Riccia crystallina*, *Ricciella fluitans*, *Ricciocarpus* natans*, *Corsinia marchantioides*, *Fegatella conica*, *Preissia commutata*, and *Anthoceros laevis*, also from isolated leaves or leaf-fragments in *Haplomitrium Hookeri*, *Plagiochila asplenoides*, *Lophocolea bilentata*, *Chiloscyphus polyanthus*, *Lophozia Mulleri*, *Porella platyphylla*, *Frullania dilatata*, and *Lejeunea serpyllifolia*. To the cases observed by the writers mentioned, the writer can add the following, in which adventive shoots were formed as the result of cultivating severed thallus-or leaf-fragments on damp sand or filter-paper:—*Riccia glauca*, *Reboulia hemispherica*, *Aneura multifida*, *A. pinnatifida*, *A. latifrons*, *A. pinguis*, *Pellia epiphylla*, *P. calycina*, *Monoclea Forsteri*, *Cephalozia bicuspidata*, *Lepidozia reptans*, *Scapania undulata*, *S. nemorosa*, *Diplophyllum albicans*, *Radula complanata*. In *Riccia* and *Reboulia*, the new shoots were found to arise from the dorsal chlorophyll-bearing tissue as well as from the ventral colourless tissue of the thallus-fragments. This was found by Schostakowitsch to be the case in *Corsinia*, though he states that in *Riccia crystallina* the new growths proceeded only from the ventral surface of the midrib.

In addition to the important generalisation proposed by Vöchting, namely, that in practically every living cell of the Liverwort-gametophyte there resides a latent capacity for regenerating the entire shoot, some other interesting results have been arrived at by the observations of Goebel and Schostakowitsch. Goebel² has shown that, at any rate in the Jungermanniales, the

¹ Schostakowitsch, W., Ueber die Reproductions-und Regenerationserscheinungen bei den Lebermoose. *Flora*, 1894 (Erg.-Bd.), pp. 350—384.

² Goebel, K., Ueber die Jugendzustände der Pflanzen. *Flora*, 1889, p. 15; Ueber die Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung. Sitz.-Ber. d. Kais. Bayer. Akad., 1897.

young shoot arising from a germinating gemma is formed in exactly the same manner as that proceeding from a germinating spore of the same species. In the majority of the leafy forms, the germinating gemma, like the germinating spore, usually gives rise to a "germ-tube," a slender filament at the distal end of which the young leafy shoot is developed. On the other hand, in *Aneura*, *Radula*, *Frullania*, and the Lejeuneae, the formation of a germ-tube is suppressed; the germinating spore or gemma of *Aneura* gives rise to a flattened ribbon-like outgrowth, the distal end of which is from the first occupied by the two-sided apical cell of the shoot, whilst in *Frullania*, *Radula*, and the Lejeuneae, the gemma exactly resembles the protonema arising from the spore, forming a discoid cell-mass, from the margin of which the leafy shoot takes its origin.

As regards the influence of external conditions on the formation of adventive shoots from excised portions of the Liverwort-gametophyte, the writer has found that, both in the thalloid and the foliose forms investigated, regeneration takes place in darkness as well as in light, but that the shoots formed in the dark show only feeble growth. This was observed in *Reboulia hemispherica*, *Preissia commutata*, *Marchantia polymorpha*, *Lunularia cruciata*, *Fegatella conica*, *Pellia epiphylla*, *Lophocolea bidentata*, and *Scapania undulata*; a similar result was obtained by Heald¹ in the case of *Lophocolea*. Schostakowitsch was unable to obtain regeneration in cultures of severed leaves of various Jungermanniales which he kept in darkness, though Klebs² found that in *Lophocolea* the leaves produced new shoots from the marginal cells when placed in weak light, whilst spores grown under similar light-conditions produced germ-tubes but no leafy shoots. Schostakowitsch found that no regeneration occurred in detached leaves which were cultivated in air deprived of CO₂, and concluded from this negative result that light does not exert a specific influence on the regeneration-processes, which failed to take place in this case on account of the lack of plastic food-materials.

APOSPORY.

Apospory, or direct origin of the gametophyte from the vegetative tissue of the sporogonium without the intervention of the spore itself, has been observed to take place in a number of Mosses, when the sporogonium has been detached and cultivated in

¹ Heald, F. de F., Gametophytic Regeneration as exhibited by Mosses, etc. Inaug.-Diss., Leipzig, 1897, p. 21.

² Klebs, G., Ueber den Einfluss des Lichtes auf die Fortpflanzung der Gewächse. Biol. Centralblatt, Band. 13, 1893, p. 649.

fragments or entire (*Ceratodon purpureus*, *Hypnum cupressiforme*, *H. molluscum*, *Amblystegium serpens*, *Bryum caespiticium*), or even whilst the sporogonium remains attached to the Moss-plant (*Funaria hygrometrica*).¹ Lang² has recently shown that apospory occurs in *Anthoceros laevis*. He found that on cutting up the sporogonia and laying them on damp sand, green outgrowths arose from the surfaces and cut ends of the fragments. These outgrowths frequently bore rhizoids and strongly resembled the young plants formed from germinating spores. Sections showed that these shoots were usually developed from the hypodermal layers of the capsule, and that each arose from a single cell.

The writer has made numerous cultures with a view to ascertaining whether this phenomenon occurs in other Hepaticae. Young capsules of *Pellia epiphylla*, *P. calycina*, *Fegatella conica*, and *Lophocolea bidentata*, were dissected out and portions of the seta and of the capsule-wall (in the latter case the spore mother cells or the young spores were as far as possible removed by means of a camel-hair brush) were grown on damp sand. In no case, however, was any outgrowth observed; the cells grew in size, and, in the case of the pieces of capsule-wall, remained green for some weeks, but ultimately became withered and discoloured. The writer hopes, however, to resume the search in the autumn, when young sporogonia are again available, for in view of Lang's discovery of apospory in *Anthoceros*, there seems to be a strong probability that this phenomenon may be induced in other forms, especially as in most cases the cells forming the wall of the young capsule contain abundant chlorophyll, which is at a later stage lost, together with the other cell-contents, when the formation of ring-thickenings takes place.

In conclusion, the writer desires to acknowledge his obligations to the following gentlemen, who have generously sent him material, in many cases consisting of living plants:—Mr. P. Furley, Aberystwyth; Mr. W. Ingham, York; Mr. J. H. Mitchell, Bradford; Mr. W. H. Pearson, Manchester; Mr. M. B. Slater, Malton; and Mr. G. Webster, York.

¹ Correns, C., Untersuchungen über die Vermehrung der Laubmoose, 1899, p. 421, and papers by Stahl, Pringsheim and Brizi, there cited.

² Lang, W. H., On Apospory in *Anthoceros laevis*. *Annals of Botany*. Vol. 15, 1901, p. 503.

THE facts of mitosis have been studied, to a greater or less extent, in almost all the great groups of the vegetable kingdom. The mosses, however, form a notable exception to this statement. This neglect is probably due, partly to the small size of the nuclei in these plants, and partly to the technical difficulties which have to be surmounted.

When we recollect the interesting results which the study of the cytology of the neighbouring group of liverworts has yielded in the hands of Prof. J. B. Farmer it appears all the more desirable that an effort should be made to trace the processes of mitosis in the Musci even in the face of the difficulties which are presented.

In the present note I wish to call attention to a rough but simple method by which the distribution and number of the chromosomes in the dividing cells can be studied with the greatest ease. Whilst examining the behaviour of the spore-mother-cell wall of *Funaria hygrometrica* toward different reagents I teased out a preparation of spore mother-cells into a physiological salt solution in which the living and unaltered cell could be studied. It could be obscurely seen that the nuclei of the mother-cells were undergoing mitotic division and with care it was even possible, dimly to make out the chromosomes. I now ran a little 1% solution of KOH containing a trace of Congo-red under the cover glass. Immediately the chromosomes, which before could only be indistinctly seen, stood out with remarkable clearness. By this means it was possible not only to follow their distribution but also to ascertain their number with absolute certainty.

The centre of the dividing spore mother-cell is seen to be occupied by four, comparatively long, rod-shaped chromosomes. By the division of these bodies eight daughter-chromosomes are formed and these separate from one another in two groups so that four daughter-chromosomes travel to each pole. Whether these immediately split again to form the chromosomes of the special mother-cells or whether the daughter-nuclei are first reconstructed, was not followed in these preparations. The appearance of both mother and daughter-chromosomes, which have been subjected to this treatment, is coarsely and irregularly granular. An examination of properly fixed capsules of *Funaria* by means of the more approved methods of microtechnique is in progress and I hope before long to describe some of the cytological features in the development of the spores of this plant in greater detail.

RUDOLF BEER.

AN EXPERIMENT IN ECOLOGICAL SURVEYING.

It may be of interest to many of our readers to know of an experiment in ecological surveying by a number of advanced students, recently carried out by the Botanical Department of University College, London.

The locality chosen was Eastern Norfolk. Here, in the well-known "Brôad" region, one has comparatively large stretches of undrained marsh, bordering on the shallow lakes or Broads and the rivers with which they are connected. In places these marshes pass gradually into the adjacent Broads, which tend to be filled up by the invasion of the marsh-plants if they are not kept clear by dredging and reed-cutting. These marshes are practically at sea-level, and in some places, where they approach very near to the coast, they are only separated from the sea by a barrier of blown sand. This sand forms typical dunes bearing the regular sand-flora for considerable stretches of coast. On the land side the sand is blown over the fresh-water marsh in a thin layer, and here the flora is transitional between sand and marsh.

Thus there exists in E. Norfolk both freshwater and sand floras largely undisturbed by cultivation, so that the natural "associations" or communities of plants are well seen.

The method adopted on the recent expedition was first to familiarise the members of the party with the type of scenery and the constitution of the marsh and water flora by sailing through a part of the country, visiting the marshes and collecting at intervals; afterwards two or three days were spent in a selected limited area which shewed a more or less typical development of the marsh and water associations. During the whole time the party lived and worked on two yachts, which formed a very satisfactory mobile base. Finally two days were spent in examining the flora of the sand dunes on a part of the coast.

Collections as complete as possible were made of the plants on the areas specially studied, the different "associations" were recognised and their boundaries approximately traced, or, in other cases, "sections" were made through the area in a direction transverse to the "strike" of the formations, the inclination of the ground, if any, the character of the soil, the water-level, and the dominant and subordinate species being noted at different points of the section. An interesting section was in this way made for instance through the "rand" or undrained marsh bordering on one of the

In their recently published and excellent book on the Morphology of Angiosperms, Drs. Coulter and Chamberlain devote a chapter to the palaeobotanical records of Flowering plants.¹ These authors, while commenting on the unsatisfactory nature of the available data, endeavour to give a summary of such testimony as we possess bearing on the phylogeny of the Angiosperms. The evidence is, I believe, even more unsatisfactory and less trustworthy than their treatment of it implies.

The most valuable palaeobotanical discoveries made in recent years are those which are based on the study of petrified fragments of Palaeozoic plants. Attention has therefore been concentrated on this branch of the Science. The less satisfactory and more difficult quest for evidence bearing on the ancestry of Angiosperms has, in consequence, been almost completely neglected. There are undoubtedly many serious difficulties to be considered in approaching the study of fossil Flowering plants; but we have spent our time in magnifying the unpromising features of the work instead of testing the capabilities of the available material.

The data quoted by Coulter and Chamberlain and by other writers have in many cases been compiled by authors whose lack of botanical knowledge renders their records of doubtful value, if not positively misleading and pernicious.

To quote one case: Drs. Coulter and Chamberlain refer to various Dicotyledons of Lower Cretaceous age, which it has been customary to refer to as Proangiosperms and to regard as comprehensive types. These so-called Proangiosperms are, I believe, in many instances of no botanical value and their designation by so alluring a title is not justified by the facts. Before we can hope to draw conclusions from fossil forms obtained from the oldest rocks in which undoubted Angiosperms occur, we must exercise the greatest care in sifting evidence and in eliminating all records that cannot be accepted with confidence.

My aim is not only to draw attention to the more or less worthless character of much of the material on which far-reaching conclusions have been founded, but to suggest that one of the most pressing needs is a thorough revision of fossil species from Cretaceous and Tertiary rocks. The work is laborious and extensive and beyond the power of the great majority of botanists to undertake single-handed. We require an organised exploration of the later plant-bearing strata and of the wealth of material already collected, which should be taken in hand by experienced palaeobotanists in conjunction with botanists who possess a wide and accurate knowledge of recent Angiosperms. I am convinced that the study of fossil Flowering Plants is well worthy of attention, and if undertaken by men who well recognise the limitations both of the capabilities of the material and of their own unaided power of identifying fragmentary fossils, it is a study that will yield results of the greatest importance. It would not be difficult to obtain the assistance of experienced systematists to criticise determinations and to co-operate in the determination of species: a greater difficulty is to find workers who are willing to devote a considerable amount of time to a laborious task and to enlist the services of specialists in the determination of their material.

I have ventured to write this letter in the hope that it may be the means of obtaining suggestions as to how the critical examination of Cretaceous and Tertiary Angiosperms may best be undertaken.

Botanical Laboratory,
Cambridge,

Nov. 9th, 1903.

I am,

Yours faithfully,

A. C. SEWARD.

¹ *Morphology of Angiosperms*. J. M. Coulter and C. J. Chamberlain. Chapter XIV. (New York, 1903).

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